HOLOCHOANITES ARE ENDOCEROIDS

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INTRODUCTION

The Holochoanites may be defined as those cephalopods in which the septal necks are so elongated that they extend from the septum of which they are a part and a prolongation, apicad to the next septum, or even farther. Hyatt (1884) first regarded the Holochoanoidea as one of two major divisions of the Nautiloidea. Later (1900) he replaced his other division, the Ellipochoanoidea, by four divisions the Orthochaonites, Cyrtochoanites, Schistochoanites and Mixochoanites, and changed the name Holochoanoidea to Holochoanites for uniformity. In the meantime, further study caused him to modify the contents of the holochoanitic division materially. Some genera originally placed in this group, such as *Trocholites*, proved upon further study to possess ellipochoanitic septal necks. The genus *Aturia*, while properly holochoanitic, was removed because it was recognized that it represented a development of elongated septal necks in Tertiary time, which was obviously quite unrelated to that of other holochoanitic cephalopods, few of which survived the close of the Ordovician. Miller and Thompson (1937) showed that the elongation of the septal necks in *Aturia* was a secondary feature and the ellipochoanitic ancestry was indicated by the retention of connecting rings. It was believed that the Holochaonites proper contain cephalopods in which the long necks were primitive, and no connecting rings were developed.

Unfortunately Hyatt does not seem to have committed himself on his ideas concerning the relationship of the Holochoanites with other cephalopods. It is not clear whether this was because of his preoccupation with the phyletic significance of early stages and the controversy that developed about the origin of the Ammonoidea and their relationship to the Nautiloidea, or whether he was as much perplexed by the problem as have been those of us who have come after him in the study of cephalopods. Two lines of evidence seemed at the time to suggest the primitive nature of the Holochoanites. First, the true holochoanitic cephalopods appeared to be concentrated at the bottom of the Paleozoic; only a few discouraged types managed to continue after the close of the Ordovician. Second, a morphological comparison seemed to indicate that a siphuncle wall composed of a single structure, the septal neck, was logically simpler and more primitive than one in which the neck was short and was supplemented by a connecting ring. Indeed, the belief was once suggested that the connecting ring developed as a differentiation of a part of the septal neck. Ruedemann (1905) suggested a possible transition from the holochoanitic to the ellipochoanitic condition by shortening of the septal neck and development of the connecting ring from the endosipholining.

Thin section investigation, however, has presented evidence that holochoanitic structure is not primitive, but that the Ordovician holochoanites developed from ellipochoanitic cephalopods, and retain connecting rings as evidence of their ancestry (Flower, 1941).

The term endoceroid has been variously, and sometimes loosely used but is probably best restricted to cephalopods with relatively large and tubular siphuncles, the interiors of which are occupied by endocones (Flower, 1941). As thus defined it excludes the Ellesmeroceratidae which lack endocones, although from the superficial similarity of the siphuncle wall of *Ellesmeroceras* and true endoceroids, that genus has been considered as an endoceroid by more than one student of the group.

Hyatt (1900) erected the Endoceratida, which has essentially the scope of our Endoceroidea, as a division of the Holochoanites. He regarded it as essentially holochoanitic, a conclusion which it is necessary now to dispute, and suggested that the group might contain cephalopods without organic deposits in the siphuncle. All genera placed in the Endoceratida, however, do contain endocones. Ruedemann (1906) in reporting holochoanitic structure in *Cyclostomiceras* and *Protocycloceras*, believed that they were primitive in this respect, but did not transfer them to the Holochoanites as would appear necessary by definition.

More recent studies have shown that holochoanitic structure is not as widespread as was formerly supposed. Foerste's earlier papers contain many allusions to supposedly widespread holochoanitic siphuncles in pre-Chazyan cephalopods. Several times he asserted the belief that all Canadian and Ozarkian cephalopods were holochoanitic, and on the strength of this premise erected at least one new genus, *Levisoceras*, which he separated as an Ozarkian holochoanitic shell from the ellipochoanitic *Cyrtocerina* of the Ordovician. Further investigations caused him to reject this hypothesis. However, it is a fact that the siphuncle walls of these older cephalopods are often thicker and are more persistently preserved than are those of their younger relatives, and anyone who has seen Tarphyceratidae with a series of camerae completely destroyed except for the siphuncle, can readily understand how Foerste supposed such siphuncles to be composed of the relatively strong septal necks instead of the connecting rings, which in younger cephalopods are often fragile, so fragile indeed that they are often wanting. Indeed, they are practically unknown in some genera, as in *Leurocycloceras* and the Silurian species assigned to *Heracloceras*.

Kobayashi (1935, 1935A, 1936) in a study primarily based upon new morphological evidence supplied by Asiatic cephalopods, found that some shells which are typical endoceroids, as defined above, were not holochoanitic. He proposed a phyletic scheme (Kobayashi, 1935, p. 750) which involved first of all the concept that the endoceroid was not primitive, but was highly specialized. He regarded holochoanitic structure as a specialization, but an early specialization, and interpreted his ellipochoanitic endoceroids as individual departures from a dominantly holochoanitic stock. He regards the Plectronocertaidae as possessing unstable siphuncles which vary from cyrtochoanitic to orthochoanitic. He regards his family Ellesmeroceratidae, however, as varying from holocohanitic in *Ellesmeroceras* to ellipochoanitic in *Clarkeoceras*. The line containing the ellesmeroceroids, the piloceroids and endoceroids, is regarded as dominantly holochoanitic. At three points, the Chilioceratidae, Baltoceratidae and Troedssonellidae, independent transitions from holochoanitic to ellipochoanitic siphuncles are potsulated. A second main line is of somewhat less definite origin. In his diagram, Kobayashi traces it to an unknown ancestor of the Plectronoceratidae but, in his text, notes that it may also have come from the Ellesmeroceratidae. He regards this line as primitively holochoanitic for, branching from it, he places the supposedly holochoanitic Protocycloceratidae and Wolungoceratidae, prior to the point at which he indicates a transition from holochoanitic to ellipochoanitic structure. Beyond this point the line splits producing the orthochoanitic "Orthoceratidae" on one hand and the cyrtochoanitic "Actinoceratidae" on the other.

Of the Protocycloceratidae Kobayashi says: "On the other hand I am inclined to recognize that *Protocycloceras* or *Orygoceras* is a Clycloderatidae or an Orthoceratidae with a holochoanitic siphuncle in which the evolution in reference to the septal character is retarded."

Later investigations support Kobayashi's main thesis of the specialized nature of the Holochoanites but show that they are even more restricted than Kobayashi believed at that time.

Schindewolf (1942) has presented a general concept of nautiloid development which is unfortunately characterized by rather vague definitions of the groups

concerned. This has previously been discussed by the writer (Flower, 1946, p. 72). Recently much new information on the older cephalopods has been presented, (Ulrich, Foerste, Miller and Furnish, 1942; Ulrich, Foerste and Miller, 1943; Ulrich, Foerste, Miller and Unklesbay, 1944) but the chert which replaced the substance forming the bulk of the material was not suitable for close morphological study, and the classification is rather generalized, the advances in knowledge of the structure are not great, and little attention is given to the important problems of phylogeny. (See Flower, 1946, p. 73–74).

Investigations on the part of the writer showed that much new information awaited discovery in the siphuncle walls of these older cephalopods. The more important of these results were published (Flower, 1941, 1941a), but much information was omitted as seemingly irrelevant. Thin section study showed that many of the supposedly holochoanitic cephalopods possessed instead ellipochoanitic siphuncles. This is true of the supposedly holochoanitic *Protocycloceras, Baltoceras, Ellesmeroceras* and *Proterocameroceras.* The evidence of the sections then at hand indicated that many, perhaps most pre-Chazyan cephalopods which were supposedly holochoanitic had instead short septal necks supplemented by connecting rings which were thick enough that they resembled septal necks to a very deceptive extent in opaque sections. Thin sections of well preserved material would show the difference at once. Further, it was found that the connecting rings were often not homogeneous, but developed either a pattern of different layers, or a pattern in which dense and apparently amorphous material termed the eyelet, tended to concentrate in the tip of the ring. The beginning of holochoanitic structure was not definitely placed, but study of Ordovician endoceroids indicated that (1) no longiconic endoceroids prior to the Chazyan possessed good evidence of holochoanitic structure, (2) the holochoanitic septal necks of Chazyan and younger endoceroids were supplemented by a connecting ring which usually agreed with that found in many Canadian ellipochoanitic cephalopods in possessing an eyelet. From these facts it was concluded that the holochoanitic endoceroids developed from ellipochoanitic types which reached their acme in the Canadian, and that the retention of the connecting ring was clear evidence of their ellipochoanitic ancestry. Further investigation indicated strongly that the ellipochoanitic ancestors were properly endoceroids, and that neither the older endoceroids nor their ancestors, the ellesmeroceroids achieved necks long enough to be considered properly holochoanitic. Additional evidence has led to the present statement of these conclusions in the more forceful terms embodied in the title of the present work, and has made possible the presentation of more evidence and the tracing of the phylogeny in more detail than the earlier evidence warranted. The earlier conclusions of the writer (Flower, 1941) were necessarily presented in somewhat general terms. A later brief statement of the phylogeny was included in the introductory portion of the study of the Cincinnatian cephalopods (Flower, 1946, p. 74–90), but the intention of this exposition was to present the evolutionary background of the Upper Ordovician cephalopod faunas, and most of the new evidence bearing upon the problem was passed over or stated only briefly.

PHYLOGENY

The oldest cephalopods comprise the endogastric cyrtocones of the Plectronoceratidae which grade without any precise boundary into the orthoconic cephalopods of the Ellesmeroceratidae. While many genera and species are now known, due to the work of Kobayashi in Asia, and to Ulrich, Foerste and Miller (1942), Ulrich, Foerste, Miller and Unklesbay (1944) in America, details of internal structure are known from only a very few of the specimens. Most of the American material consists of chert internal molds and replacements which are not suitable for a proper morphological study. Some, but plainly not all, of the members of this group possess diaphragms, but it is to be feared that some of the structures

termed pseudodiaphragms are not natural but are either adventitious structures or the appearance presented by the rather thick connecting rings in sections which approach close enough to the wall of the siphuncle to intersect it tangentially. These cephalopods have septal necks which are ellipochoanitic or often aneuchoanitic, that is, possessing septa which are scarcely bent apicad at the point where they meet the connecting rings. Study of a considerable suite of specimens has led the writer to reject the holochoanitic siphuncle wall and the presence of diaphragms which Kobayashi (1935a, p. 22, Fig. II), represents for the Ellesmeroceratidae.

The next step in development is that represented by the Proterocameroceratidae (Flower, 1946, p. 80). The siphuncle wall may be as primitive as that of the Ellesmeroceratidae, but within the siphuncle are developed endocones, making these cephalopods true endoceroids. Much variation has been noted in the length of the septal necks in this group; Necks vary from those which are aneuchoanitic to those which approach but do not quite attain the holochoanitic pattern. Likewise, there is here variation between the banded type of connecting ring and that showing the eyelet, with important transitional stages showing the close relationship of these seemingly opposed structural types. There is likewise variation in the form of the endosiphuncle, which may be simple, as appears to be the rule among the Middle Canadian types, or may become quite complex as in the Upper Canadian *Proterocameroceras* or the sole Chazyan member of the stock, *Meniscoceras*.

The next stage in advancement is marked by two contemporaneous modifications, first an elongation of the septal necks until a holochoanitic condition is reached, and second, a tendency for both the shell and the siphuncle to expand very rapidly, although this may be followed in the mature shell by a living chamber which is more or less contracted, so that a typical breviconic shell is eventually formed. This change has reached its acme in the true Piloceratidae. It is believed that some of the Asiatic piloceroid shells may supply a transition from the Proterocameroceratidae to the Piloceratidae in respect to both of these important features. Certainly some of these shells, as *Coreanoceras* and *Manchuroceras*, are only moderately breviconic. Further, it is just among these forms which are transitional in regard to the shell form, in which the rate of expansion of the conch is mainly concerned, that one finds the ellipochoanitic siphuncles. However, Kobayashi has described structures in the endosiphuncles of these cephalopods which indicate that they have undergone very marked specializations of their own. Admittedly, a number of these cephlaopods require further study before their precise position in the phyletic scheme can be definitely established.

At the close of the Canadian the Piloceratidae disappear and the Proterocameroceratidae are represented only by one genus, *Meniscoceras* which penetrates as high as the Middle Chazyan. Their place is taken by slender endoceroids which are regarded as descendants of the Piloceratidae, from which they inherit a tendency for the siphuncle to expand markedly in the early growth stages so that it may occupy the entire apex of the shell, and holochoanitic septal necks which still retain connecting rings. The combination of a slender shell and holochoanitic septal necks has been used as the criterion for the family Endoceratidae. The writer previously believed that some members of this family lost the connecting ring which was retained in the more generalized endoceroids. Further examination of thin sections has, however, indicated that the loss of the connecting ring in those specimens which lack it is more probably the result of solution under unfavorable conditions of preservation. The Piloceratidae-Endoceratidae series is essentially a tachygenetic sequence. Reduce the pattern of a piloceroid phragmocone in size, add to the end a shell in which the siphuncle and conch are both slender, and the resultant type is essentially a *Nanno*, such as persists from the Chazyan to the Richmond. Reduction of the recapitulatory swollen siphuncle of a *Nanno* results first in the inflated, but still swollen, siphuncle of a *Suecoceras*, and finally in the tubular siphuncles found in those cephalopods to which the generic names *Cameroceras* and *Foerstella* have been applied.

THE ELLESMEROCEROID COMPLEX

It is necessary to begin the detailed tracing of structural changes with a survey of the ellesmeroceroids, which are properly the ancestors of the endoceroids.

The ellesmeroceroids are primitive cephalopods which were the dominant and perhaps the exclusive representatives of the nautiloids up to the close of the Lower Canadian (Gasconade, Wanwanian), only a few genera and species surviving into later faunas. Although exceedingly variable in form, these cephalopods are readily recognized by their small size, very closely spaced septa, the dominantly compressed section, the attendant development of lateral lobes of the sutures, and the large ventral siphuncle which is devoid of endocones. Much remains to be learned concerning the crucial morphological features of these cephalopods, but many species have been described (Kobayashi, 1933, Ulrich, Foerste and Miller, 1943; Ulrich, Foerste, Miller and Unklesbay, 1944).

Shells of this group exhibit almost every gradation in form from strongly curved endogastric cyrtoceracones to orthoceracones. The shells likewise show all gradations between those which expand very rapidly to those which are essentially tubular. The mature living chamber and apertures may be simple, or may be variously constricted and contracted. The extreme of contraction is reached in *Buehleroceras* and *Burenoceras*, which develop apertures strongly suggestive of the younger *Phragmoceras*. The section is dominantly compressed, often strongly so. However, some species of *Ellesmeroceras* are circular in section, and *Pachendoceras* is probably a depressed ellesmeroceroid rather than an endoceroid. The two supposed spicula which have been figured in this genus are open to other interpretations. One is probably adventitious (Ulrich, Foerste, Miller and Unklesbay, 1944, Pl. 64, Fig. 1), and the other (Ibid., Pl. 61, Fig. 4), represents instead the apex of the siphuncle. The sutures may be essentially transverse or may be inclined orad on the dorsal (antisiphonal) side. Lateral lobes are commonly developed, but all gradations between straight and deeply lobed sutures occur, the variation generally corresponding to the development of a compressed cross section.

In spite of wide form variation, the group is a homogeneous one. Many of the species lie so close to the boundaries of the genera as at present defined, that their reference to either one to the exclusion of the other is sometimes extremely difficult. While taxonomic difficulties may easily result, it is clear that the ellesmeroceroids represent a homogeneous but exceedingly plastic group, and one which expanded rapidly in the early Canadian, possibly because it lacked ecological competition.

Attempts to express the diversity exhibited by those cephalopods by the use of several families, have not been very successful. Kobayashi (1933, 1935a) divided these cephalopods into the Plectronoceratidae and Ellesmeroceratidae, apparently mainly on the basis of characters of the siphuncle. He regarded the Plectronoceratidae as varying from orthochoanitic to cyrtochoanitic (Kobayashi, 1933) and the Ellesmeroceratidae as grading from orthochoanitic to holochoanitic (Kobayashi, 1935a). The sections upon which the cyrtochoanitic condition is based are unfortunately rather faint,but the conclusion may be tentatively accepted until better evidence is at hand. Flower (1941a), found *Ellesmeroceras* to be aneuchoanitic and not holochoanitic, as Kobayashi believed, a condition which has subsequently been substantiated by unpublished thin sections.

Ulrich, Foerste and Miller (1943) and Ulrich, Foerste, Miller and Unklesbay (1944) divided these ellesmeroceroids into several families on the basis of an exceedingly artificial classification. Orthoceracones were placed in the ill-advised Orthocerotidae, endogastric cyrtoceracones in the Cyrtendoceratidae and straight brevicones in the Cyclostomiceratidae. Flower (1946) pointed out that the cephalopods of the Lower Canadian formed a closely knit group, and the genera distributed among these three families had much more in common, and less in common with other genera placed in those same families, than this current classifi-

cation would indicate. *Cyrtendoceras* is described as a holochoanitic endoceroid. If so, these endogastric Wanwanian cyrtoceracones should not be placed with it, for they have neither holochoanitic siphuncle walls nor endocones. The family, as thus employed, has no genetic significance. A much closer approach to a taxonomic expression of relationship can be attained by employing the Plectronoceratidae for the endogastric cyrtoceracones and the Ellesmeroceratidae for the orthoceracones of this group. Even so, difficulties are encountered, for there is no clear boundary between these two families. *Eremoceras* and *Ectenoceras* lie essentially upon the tenuous boundary between the orthoceraconic and cyrtoceraconic, and could be placed in either family with about equal justification. For these reasons it seems wisest in the present state of our knowledge to discuss the two families together.

Actual evidence as to the structure of the siphuncles in these forms is very meagre. Kobayashi (1933) published excellent sections of the Manchurian *Multicameroceras*, *Sinoeremoceras*, and *Wanwanoceras*. Unfortunately the limestones showed only rather faint color variation and the photographs were strongly retouched for illustration. Under such circumstances, interpretation of the original structure is extremely difficult. A connecting ring projecting within the siphuncle wall, after the manner of those of *Eothinoceras*, might present a very similar effect without being properly cyrtochoanitic. Unfortunately, it seems necessary to regard with doubt the adoral expanded connecting ring which Kobayashi (1935a) figured for *Plectronoceras*. Ulrich, Foerste, Miller and Unklesbay (1944) suggest that the structure figured may be adventitious and that *Plectronoceras* may have lacked connecting rings. The absence of connecting rings is a conclusion which we are reluctant to accept in view of their universal and very strong development in Lower Canadian cephalopods, but certainly is supported by the present evidence.

The siphuncle wall of *Ellesmeroceras* was figured by the writer (Flower 1941a). The septal necks are very short and are supplemented by thick connecting rings. Possibly some structural differentiation may have taken place within the ring, but the sections studied so far suggest such variation without being clear enough to demonstrate it conclusively. Subsequent thin sections of other species of *Ellesmeroceras* show similar septal necks, but fail to show the original state of the connecting ring clearly. Ulrich, Foerste and Miller (1943, p. 92), have illustrated a very clear section of a *Clarkeoceras*, showing a relatively long septal neck and a thick connecting ring. Except that no zonal differentiation in the ring is indicated, this section is very similar to that of our *Cyptendoceras* shown in Fig. 1c.

The evidence as to the structure of the siphuncle wall in these cephalopods is quantitatively meagre, but indicates aneuchoanitic to rather long ellipochoanitic necks, supplemented by rather thick connecting rings.

Within the siphuncles of some of these cephalopods diaphragms have been reported. The actual evidence of diaphragms is, however, again very meagre. The structures which Kobayashi (1933) figured as pseudodiaphragms in the Plectronoceratidae are so faint that they may well be inorganic. In America, the evidence for diaphragms crossing the siphuncle rests upon a mere handful of specimens. The structure is shown by one specimen of *Stemtonoceras elongatum*, two of *Levisoceras*, sp., and several of *Robsonoceras robsonense*. My own material has so far yielded clear diaphragms only in an undescribed species of *Dakeoceras*. Hyatt (1900) first reported these structures in *Diphragmoceras*, but the type species has never been figured, and only inadequately described. Clarke described diaphragms in *Clarkeoceras newton-winchelli* but Ulrich, Foerste, Miller and Unklesbay reported that the evidence for these structures is inconclusive.

A number of chert internal molds by which much of the American material of Gasconade age is represented, show siphuncle fillings which terminate rather abruptly in bluntly rounded tips. This may signify that infiltration of the matrix

into the siphuncle from the living chamber was stopped adapically by a diaphragm, the remainder of the siphuncle being filled only with inorganic calcite and later lost by solution along with the original shell parts. This interpretation is, of course, hypothetical. However, the postulation of diaphragms as an explanation of this phenomenon presents a logical answer to the problem set by these bluntly rounded siphuncle fillings. An organic rather than an inorganic cause is suggested by the occurrence of such abruptly terminated fillings in a group of cephalopods which form both a taxonomic and a stratigraphic unit, the ellesmeroids of the Lower Canadian. Such siphuncles have been illustrated for *Levisoceras*, *Oneotoceras*, *Caseoceras* and the Middle Canadian *Cumberloceras*, and are suggested, though less conclusively, in still other genera.

Admittedly, the meagre data at present do not supply a good basis for understanding the role of diaphragms in growth or function. Good evidence of the structures is so rare that it is uncertain whether they occur only in isolated individuals, whether they developed in only a few species, or whether they may be characteristic of genera which might even be set apart in a family by themselves. Actinosiphonate structure long presented the same problem, and the material by which it could be studied and evaluated was much more abundant than that showing diaphragms.

The limestones in America which yield ellesmeroceroids have not been widely studied faunally. Faunas under investigation by the writer promise to yield much information on the siphuncles of a number of the genera, but in their study the same difficulties are encountered as in the Wanwankou limestone of Manchuria and Korea; color differentiation is faint and makes it difficult to distinguish organic from inorganic features. The ellesmeroceroids clearly fail to show holochoanitic structure, and possess instead short necks and rather dense thick connecting rings. Diaphragms occur in the group, but are rare and of uncertain significance.

The genera which constitute the ellesmeroceroids have been summarized by the writer (Flower, 1946, p. 75–78). They include the Cambrian *Plectronoceras*, the Lower Canadian genera *Shelbyoceras*, *Dakeoceras*, *Burenoceras*, *Buehleroceras*, *Oneotoceras*, *Levisoceras*, *Caseoceras*, *Conocerina*, *Eremoceras*, *Ectenoceras*, *Ellesmeroceras*, *Walcottoceras*, *Robsonoceras*, *Endocycloceras* and *Albertoceras*. *Cumberloceras* and *Smithvilloceras* represent survivals of the stock in Middle and Upper Canadian, and *Cyrtocerina* and probably *Shideleroceras* represent the last survivors of the group persisting to the Richmond. Separate families have been erected for *Buttsoceras*, *Cyrtocerina* and *Shideleroceras*. The proper placing of the remainder in the *Plectronoceratidae* and *Ellesmeroceratidae* must await further study of the structure of the genera.

PROTEROCAMEROCERATIDAE

The family Proterocameroceratidae (Flower, 1946, p. 80), was erected for slender endoceroids with ellipochoanitic siphuncle walls. These are the oldest of the endoceroids and the most primitive. Their slender form sets them apart from the piloceroids, a few of which are also ellipochoanitic. The holochoanitic siphuncle wall distinguishes the Piloceratidae proper as well as the slender Endoceratidae. From the Ellesmeroceratidae the Proterocameroceratidae differ in two respects, the presence of endocones and the differentiation of parts of the connecting ring. The last difference may not be real, but only apparent, for as yet very few ellesmeroceroids have been studied from specimens well enough preserved to show this differentiation should it occur. *Ellesmeroceras bridgei* shows some indication of such specialization in the connecting ring, but the evidence is not conclusive.

Determination of the exact scope of the Proterocameroceratidae requires more information than is now available. Previously it has been assumed that all endoceroids were holochoanitic, and no detailed examination of the siphuncle wall was

undertaken. The discovery of aneuchoanitic necks and thick rings simulating necks in opaque section in *Proetrocameroceras*, (Flower, 1941), showed that a careful restudy of endoceroid siphuncle walls would have to be undertaken, preferably by the use of thin sections. Unfortunately this is made difficult by the rarity of suitably preserved material among the older endoceroids. Quite probably the Proterocameroceratidae contain all of the slender endoceroids older than the Chazyan. Certainly all of the Canadian slender endoceroids thus far studied from satisfactory material have yielded ellipochoanitic siphuncles. The number of species and genera which supply this evidence do not, it is true, make a very imposing assemblage. However, the scant evidence is unanimous in indicating ellipochoanitic structure in Canadian endoceroids. The genera in which such structure has been found include *Proterocameroceras*, *Clitendoceras* and *Cyptendoceras*. Suitable material for *Cotteroceras*, *Cyptendocerina*, *Paraendoceras* and *Mcqueenoceras* is not yet available; the extant material of these genera consists of shells which are either chert steinkerns or are extensively dolomitized so that the siphuncle wall is greatly altered. There remain generalized species which have been assigned to *Endoceras*. Sections made from such species indicate that they also are ellipochoanitic and are therefore not properly assignable to *Endoceras* or to the Endoceratidae.

The endoceroids of the pre-Chazyan have been distributed among various genera on the basis of cross section, suture pattern and form. *Proterocameroceras* was shown to be ellipochoanitic (Flower, 1941) and was therefore removed to the Orthocerotidae (Ulrich, Foerste, Miller and Unklesbay, 1944). No species other than the genotype was recognized. Other endoceroids were referred to the Endoceratidae. Straight compressed shells were assigned to *Cotteroceras*. *Clitendoceras* was used for shells which are circular, but have oblique sutures, sloping orad on the dorsum. Perhaps not enough stress was placed on the faint exogastric curvature shown by the genotype. *Cyptendoceras* was employed for depressed shells in which the sutures form ventral and sometimes dorsal lobes. *Cyptendocerina* also has ventral lobes, but the siphuncle is farther from the venter. *Mcqueenoceras* is faintly endogastric, and closely allied to *Clitendoceras*. *Pachendoceras* is employed for depressed shells with a flattened venter and transverse sutures. *Paraendoceras* is distinctive in its rather rapid expansion, approaching some of the more slender shells which have been grouped by Kobayashi with the piloceroids. The more generalized of the species assigned to *Clitendoceras* and *Cyptendoceras* approach very closely to those Canadian shells which have been placed, we think mistakenly, in *Endoceras*. A survey of the Canadian species placed in *Endoceras* shows that not one exhibits evidence of a holochoanitic siphuncle, and many lack evidence of endocones. Many are not true endoceroids, and none are demonstrably members of the Endoceratidae.

It is within the Canadian Proterocameroceratidae that evidence exists of the specialization of the connecting ring and of modifications of the septal neck approaching, but not attaining, a holochoanitic condition.

DEVELOPMENT OF THE SEPTAL NECKS

As previously shown, the meagre evidence indicates that in the ancestral Ellesmeroceratidae the septal necks vary in length, but none have been found which are long enough to be called holochoanitic. The shells which are most similar to the true endoceroids are those of the genus *Ellesmeroceras*, which, indeed, is most readily differentiated from the endoceroid by the absence of endocones. Happily, the actual morphological data is largest for this crucial genus, and indicates uniformly necks so short as to be properly aneuchoanitic. (Fig. 1A).

Within the Proterocameroceratidea, *Proterocameroceras* itself possesses aneuchoanitic necks similar to those of *Ellesemroceras* and *Eurystomites* (Flower, 1941), (Fig. 1B). *"Cameroceras" annuliferum* Flower, a species which is probably best

placed in the genus *Cyptendoceras*, although it is admittedly generalized in respect to section and sutures, shows short orthochoanitic necks supplemented by connecting rings. *Clitendoceras* has been observed to show a gradual adoral lengthening of the necks in a series of camerae. An undescribed Middle Canadian *Cyptendoceras* (Fig. 1C) shows septal necks which are essentially funnel-shaped rather than tubular. These extend far enough apicad to be at a level with the bend of the next adapical septum, but are so far removed from the septum that the condition escapes being properly holochoanitic. The septal necks of *Coreanoceras* (Kobayashi, 1935) are only slightly longer ventrally. It is perhaps significant that in this genus the condition approaches the holochoanitic without quite attaining it. Further, these same shells, though grouped as piloceroids by Kobayashi, have only moderately expanding siphuncles and phragmocones. In both respects they are intermediate between the Proterocameroceratidae and the Piloceratidae.

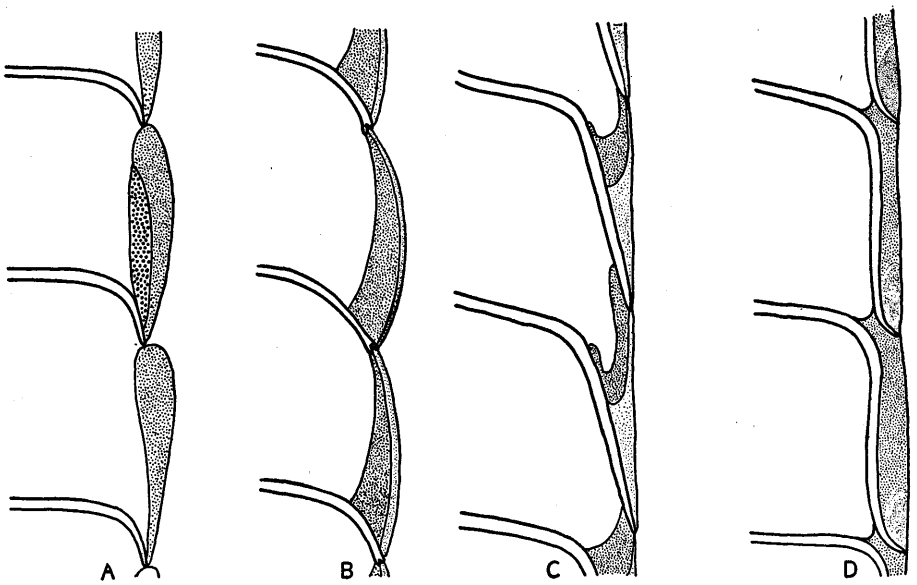

FIG. 1. Stages in development of holochoanitic spihuncle wall. A. *Ellesmeroceras*. Aneuchoanitic necks and thick rings. The middle ring shows differentiation of an outer layer suggested by *Ellesmeroceras bridgei* Flower. B. Double layer of connecting ring, as developed in *Proterocameroceras;* based on *P. brainerdi*. C. Intermediate stage, showing incipient concentration of central layer at apex, from *Cyptendoceras*. D. Development of holochoanitic necks, with concentration of dense material making up central layer in B and C at apex, forming eyelet. From *Vaginoceras oppletum* Ruedemann.

THE CONNECTING RING

The progressive series already traced on the basis of the septal neck is supported by stratigraphic evidence, but in itself would be weak without the corroborative evidence supplied by the connecting ring. The ellesmeroceroid-endoceroid line is characterized by connecting rings which are generally and perhaps uniformly thicker than those of the line containing most ellipochoanitic cephalopods. Further, connecting rings of this type show generally some sort of structural differentiation. Two distinct and seemingly diametrically opposed types of structure were found, one in which the connecting ring was divided into an inner and an outer zone, the inner (central) zone consisting of denser and finer grained material than the outer zone. In contrast, a second type was found in which the denser and finer material was concentrated at the tip of the connecting ring. The banded

types (Fig. 1B), were first noted in *Proterocameroceras* and in *Eurystomites*, the other type (Fig. 1D), to which I gave the name of eyelet, was found in *Tarphyceras* and in *Endoceras* and *Vaginoceras*. Subsequently it was found in *Cassinoceras*, and there is reason to believe that it is present in *Piloceras* also.

No great taxonomic significance could be given to these diametrically opposed types of connecting rings, for it was obviously unthinkable to unite *Tarphyceras* closely with true *Endoceratidae*, and to unite *Eurystomites* with the endoceroid genus *Proterocameroceras*. To do so would necessitate passing over the strong evidence supplied by section and ontogeny connecting *Eurystomites* and *Tarphyceras* (Hyatt, 1894) and also the evidence supplied by not only form similarity but also the structural patterns of the endosiphuncles of *Proterocameroceras* and the Endoceratidae. Obviously these two types of structure represent variations of a single fundamental structural pattern under the influence of secondary factors which worked indepednently in the Tarphyceratidae and Endoceroidea. Inspection of the nature of the materials of the connecting ring suggests that the central or innermost layer of the zonal pattern is the homologue of the eyelet in the end ceroid pattern. Both consist of dense fine grained to amorphous material, while in contrast the remainder of the connecting ring is crystaline or coarsely granular. Further, the two structures behave very differently under various conditions of preservation. Examples are known of preservation of the eyelet and the inner zone while the remainder of the ring is incomplete or altogether destroyed. When the two types of structure are viewed in relation to the septal necks some suggestion of a solution is found, for the zonal condition is found thus far only in cephalopods with aneuchoanitic necks, but where the septal necks are long, in the connecting ring, which invariably extends from the tip of one neck apicad to the tip of the next, the portion lying within the adapical neck has developed into the eyelet. This is true of *Tarphyceras*. It was not as obvious for *Endoceras*, for the entire length of the connecting ring lies within the next adapical septal neck. Why was not the entire length of the ring given over to structure of the eyelet type? An explanation is suggested by the nature of the materials concerned. If the endoceroids, as was certainly true of many other cephalopods, maintained a connection throughout life between tissues lining the camerae and those occupying the siphuncle, such a connection could have taken place only through a permeable connecting ring. The typical connecting ring was therefore assumed to be secreted within tissue (Flower, 1939), and to maintain a porous character throughout life. As a structure through which such materials must have passed, the ring must remain porous. The eyelet, however, is clearly a part of the ring which is made of dense fine grained amorphous material, which could hardly have been porous. Therefore, it is natural that such material should concentrate in that part of the connecting ring which lay within the next adapical septal neck, where, because of the solid nature of the neck opposing it externally, no metabolic connection existed. Such differentiation of materials may or may not have been completed prior to the perfection of the holochoanitic siphuncle of the Piloceratidae. However, if a metabolic connection between camerae and siphuncle was maintained in holochoanitic shells prior of course to the filling in of the adjacent part of the siphuncle by endocones, such a connection must have taken place through the adoral part of the connecting ring, passing between the septa.

How any such connection was maintained in aneuchoanitic shells with a zonal arrangement of the materials of the connecting ring is uncertain. Either no connection could have existed, or else the inner zone was more porous than was the eyelet. The nature of the material as seen in sections suggests the second explanation, but I do not consider the evidence conclusive. There is no evidence to suggest that the camerae were sealed from the remainder of the shell by delayed secretion of the inner zone; on the contrary, the inner and outer zones were either secreted together, or else the outer zone appeared after the inner one; certainly not

before. There is some indication that the outer zone may have thickened by subsequent growth, as suggested by laminae shown in the clearest of the sections. Certainly cameral tissue is a primitive, rather than a specialized, feature and one therefore presumably present in these older cephalopods. The fact that evidence of cameral deposits is nonexistent in the ellesmeroceroids and requires further study in endoceroids before its presence can be conclusively accepted is beside the point.

The faint suggestion of zonal arrangement in *Ellesmeroceras bridgei* Flower (1941a), as indicated in one segment of Fig. 1A, is not conclusive. However, it does suggest that the zonal arrangement is primitive and the eyelet structure developed from it, for the ellesmeroceroids are clearly both older and more primitive than those cephalopods known to show the eyelet.

New material, in the form of a section of an undescribed species of *Cyptendoceras* supplies evidence which forms some basis for this reasoning. The section (Fig. 1C), is intermediate in both the length of the septal neck and the arrangement of the dense material of the connecting ring, between the condition found in *Proterocameroceras* on one hand and that found in *Endoceras* on the other. The septal necks, as already noted, are nearly holochoanitic, but are widely separated because their pattern is conical rather than tubular. The intervening connecting ring is of such a nature that it can be interpreted in terms of either the zonal or the eyelet pattern being an intermediate phase connecting the two. An inner and outer zone can be clearly recognized, but the inner zone is greatly thickened adapically. Likewise, one can interpret the same section as an eyelet which is stretched orad along the inside of the main part of the ring, while the main part of the ring is thickened and somewhat folded around the bend of the septum at its adapical end.

Clear development of the eyelet pattern in an ellipochoanitic endoceroid has not been found. *Cyptendoceras annuliferum* (Flower) showed traces of the eyelet in relatively thick transparent sections. The clarity of the eylet was lost in reduction of the thickness of the section for photography. It is a curious fact that both the eyelet and the perispatial deposits of actinoceroids may be reduced to a point at which they become nearly invisible in the thinnest of sections. Unfortunately they are best displayed in sections thick enough that the contrast between calcite-replaced shell parts and the matrix are so strong that they are not suitable for photography. *C. annuliferum* displays eyelets which are essentially similar to those found in *Tarphyceras seelyi* (Flower, 1941, Pl. 1, Fig. 2, Pl. 1, Fig. 9–10).

While much more remains to be learned about the nature, function and possibilities of radial variation in clarity and distribution of the eyelet in endoceroids, the main point of the structure is that it demonstrated clearly that the connecting ring is retained in the holochoanitic Endoceroidea. This is indicated not only by the phyletic sequence postulated in Figs. 1B-D, but also by the identity of the structure of the connecting ring in *Nanno* and *Vaginoceras* with that of *Centrotarphyceras* (Flower, 1941). Prior to this, the existence of the connecting ring in holochoanitic cephalopods was not recognized. Hyatt (1900) presented a figure of *Endoceras proteiforme* (Fig. 2) showing holochoanitic necks separated by bands which are apparently morphologically distinct from them. The tip of the neck and the tip of this unidentified band are separated by areas indicated in black, which correspond to the eyelet. Hyatt never amplified the complexities of structure indicated in this diagram and his interpretation of these structures is therefore somewhat dubious. However, he never mentioned the presence of a connecting ring. Ruedemann (1906, Fig. 3, p. 413) reproduced Hyatt's figure, and showed a similar structure in *Vaginoceras oppletum* (Pl. 4, Fig. 2–3). This specimen fails to show clearly the differentiation between the septal neck and the connecting ring which arises from its tip. Without this differentiation, the structure seems to be that which Hyatt (1900) had earlier attributed to the genus

Vaginoceras. As a consequence, it is not unnatural that Ruedemann interpreted it as such, and on the basis of this structure assigned his species to the genus *Vaginoceras*. Of the dense and darker colored areas which represent the eyelets Ruedemann says: "The structure of the siphuncular wall, which is here that of a *Vaginoceras*, would suggest that the pseudosepta extend through or caused the collarlike interspace which enters between the septum where it bends into the septal neck and the septal neck of the next younger septum which at this point bends slightly outward." The structures are extremely confusing, and it was not until the species had been examined by abundant thin sections, each of which indicated the same structural pattern, that it became clear that the morphological interpretation must be revised.

The presence of a connecting ring in the holochoanitic Endoceratidae indicates a conclusion already voiced by Kobayashi on the basis of endosiphuncular structures, that the endoceroid was not primitive but highly specialized. Further, it

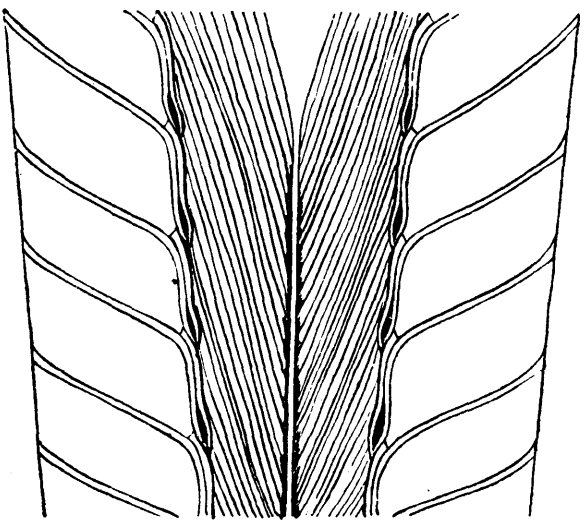

FIG. 2. Section of *Endoceras proteiforme* Hall, after Hyatt. The septal necks are shown as holochoanitic, but supplemented by other unidentified structures which correspond to the main part of the connecting ring. The adapical tips of the rings are shown as separated from the necks by black areas. These represent the eyelets, properly a part of the rings, as shown by thin sections. Within is shown the endosiphuncle, with numerous endocones terminating in an endosiphotube.

indicated that the endoceroid must have had an ancestry which was ellipochoanitic. Later investigations revealed that this ancestral phase was much more widespread than Kobayashi had realized, for it embraced not only the Plectronoceratidae, which he had shown to have short necks supplemented by connecting rings, but also the Ellesmeroceratidae and the older of the shells which had previously been assigned to the Endoceratidae. This required more a revision of a conception of morphology than one of relationship for, while it was an error to consider the Ellesmeroceratidae and the older Endoceratidae as holochoanitic, the fact remained that the structure of their siphuncle walls was practically identical, and in both groups the thick connecting ring did not simulate a septal neck very closely except in the most favorably preserved material.

Material suitable for a proper study of zonation in the connecting ring of *Ellesemroceras* has not yet been found. *Ellesmeroceras expansum* Flower (1941A, Fig. 1A-B, Pl. 1, Fig. 9, Pl. 2, Fig. 6), shows evidence of some dark material which

lies in a few of the camerae between the white calcite which has replaced the connecting ring and the white calcite which forms a chemically deposited filling for some of the camerae. This suggests the possibility of a banding of the connecting ring such as is indicated in text Fig. 1A in the upper complete segment. The transverse longitudinal section of the same species (Flower, 1941A, Pl. 1, Fig. 10), also shows a suggestion of such zonation. However, other parts of the phragmocone lack evidence of these structures and further information is needed. Material of *Ellesmeroceras* from eastern New York has thus far been found to be too extensively recrystallized to yield much additional information.

Where banding is well developed it forms a pattern in which the inner zone is fairly uniform in thickness throughout its length, while the outer zone is widest adapically. This structural pattern is fairly widespread among Canadian nautiloids, and is not by any means confined to the Proterocameroceratidae. It was figured by the writer for *Proterocameroceras* and *Eurystomites*. Ulrich, Foerste and Miller (1943), p. 56, Fig. 3B), have shown the same structural pattern in *Cyclostomiceras cassinense*. Subsequently the same structural pattern has been observed in my own material of *Onychoceras* and *Basslerоceras*. Among orthoconic types it is present in *Baltoceras*, and *Protocycloceras* shows a siphuncle wall which is probably a slight modification of this pattern. Ulrich, Foerste, Miller and Furnish have figured several siphuncles of Canadian nautilicones which appear to have this structure. *Aphetoceras attenuatum*, shown on their Pl. 25, Fig. 6, is very close to *Eurystomites*, although the resemblance is much less marked in the drawing (text Fig. 3, p. 19) of the same section. *Campbelloceras rotundum* (Fig. 10, p. 47, Pl. 50, Fig. 5) shows a suggestion of zonal development, though the irregularity of the structures is again accentuated in the drawing. Here the connecting ring in the ventral siphuncle is so thickened ventrally as to nearly fill the space between the cavity of the siphuncle and the ventral wall of the shell. Such sections suggest that the connecting ring grew after it first appeared by the addition of material to its cameral surface. Whether such deposits of the connecting ring grew outward into the camerae in *Curtoceras* is still uncertain, but such a possibility is strongly suggested by Ulrich, Foerste, Miller and Furnish (Pl. 50, Fig. 3).

Cyptendoceras sp. (Fig. 1C) is thus far the only specimen showing a combination of transitory phases of the septal neck between ellipochoanitic and holochoanitic with a transitory phase between the eyelet pattern and the presumably more generalized zonal condition. Similar conditions are to be expected in some of the Asiatic piloceroids, in particular *Kotoceras*, but the only figure of the siphuncle wall available (Kobayashi, 1936, Pl. 22, Fig. 13), is not enlarged sufficiently to show this. Further, in this specimen, which is an opaque section, differentiation of the septal neck and the connecting ring is not clear.

PILOCERATIDAE

Flower (1941) reported in *Cassinoceras explanator* (Whitfield) structures within the siphuncle which seemed to represent connecting rings, complete with the eyelet, which suggested that the siphuncle was holochoanitic and had essentially the structure observed more fully by means of thin sections in *Vaginoceras oppletum* Ruedemann. Later sections have served to confirm this view. Ulrich, Foerste and Miller (1943) p. 22, found similar structures in *Piloceras invaginatum* Salter, but did not recognize them as connecting rings. They describe them as follows: "The inner surface of the septal necks is lined by a black layer which is about 0.4 mm. thick and which terminates as a thin edge at the adapical end of each neck. The adoral portion of this black layer extends between the adoral end of a septal neck and the adapical end of an adjacent neck for a distance of about 1 mm. along the adoral surface of the septum which gives rise to the adapical neck. Along the inner surface of the siphuncle there is a discontinuous series of these black layers each one 'pinching out' at the adapical end of the septal neck which it lines."

This might almost be a description of the connecting ring shown in Fig. 1D, and there can be little doubt but that it represents an identical structure except that there is no mention of the eyelet. Indication of the eyelet is very plain in *Cassinoceras explanator.*

Happily, the presence of connecting rings within the septal necks in these two species, which are the genotypes of *Piloceras* and *Cassinoceras*, show that the Piloceratidae proper are holochoanitic.

The origin of the Piloceratidae is clearly to be sought in the Proterocameroceratidae itself. Perhaps some of the lesser known slender shells which have been considered piloceroids in Asia may supply the link. *Coreanoceras*, the only member of this group of shells for which the siphuncle wall is known, is ellipochoanitic, as shown by Kobayashi (1935a). This shell is so slender, however, that it seems it might be grouped as easily with the *Proterocameroceratidae* as with the piloceroids; certainly it differs markedly in aspect from the broadly expanded siphuncle of *Chilihoceras*, with which Kobayashi would group it.

It should be pointed out also that we have no evidence as to the position of *Chilihoceras* Grabau, *Manchuroceras* or the closely allied and probably synonymous *Liaotungoceras* Shimizu and Obata in this scheme. The endosiphunclar specializations of *Chilihoceras* described by Grabau are so remarkable that other students of cephalopods, who have, it is true, not seen the material, are a bit reluctant to accept the rather complex interpretation of the endosiphuncle which Grabau presents. *Manchuroceras* and *Liaotungoceras* were depressed siphuncles. In true Piloceratidae, in which I should include *Piloceras*, *Cassinoceras* and *Allopiloceras*, both the conch and the siphuncle are compressed. The endosiphuncular differences together with the differences in form suggest that the depressed Asiatic genera have undergone a development independent of that of the Piloceratidae, and the two lines may have separated prior to the development of holochoanitic necks. Kobayashi (1935, p. 750), idicates ellipochoanitic necks for the Chiliocerati dae, but to the writer it seems unwise to unite the strongly breviconic *Chilihoceras* with the smaller and much more slender *Coreanoceras*, which supplies the only basis for making any statement concerning the siphuncle wall.

ENDOCERATIDAE

While the origin of the Piloceratidae is somewhat obscured by lack of information concerning the structure of possibly crucial genera of Asiatic piloceroids which may supply connecting links with the Proterocameroceratidae, there is enough evidence to show that between these two families occurred the transition from the ellipochoanitic to the holochoanitic siphuncle. The descendants of the piloceroids are easier to trace.

With very few exceptions, it has been seen that the Lower Canadian, with which the Gasconade and Wanwanian are synonymous, contains the acme of the ellesmeroceroids. The Middle Canadian however, shows a maximum development of the Proterocameroceratidae. The Upper Canadian is marked by the piloceroids. The Longview limestone of Alabama furnishes one of the few exceptions. This supposedly Middle Canadian formation contains *Cumberloceras*, which is morphologically a Lower Canadian type, and also *Allopiloceras*, elsewhere confined to the Upper Canadian. Other members of its fauna are essentially Middle Canadian. I have observed similar phenomena, involving a mingling of Lower and Middle Canadian types locally in the Fort Ann region of eastern New York, but closer study has shown that due to deposition of Middle Canadian beds on an uneven erosion surface, in some places fossiliferous Lower and Middle Canadian limestones very similar lithologically, are brought into juxtaposition. So anomalous is the fauna of the Longview that it might be re-examined with this possibility in mind. At present, I am reluctant to accept it as evidence of the appearance of piloceroids in the Middle Canadian.

At the close of the Canadian the Piloceratidae disappear. The Proterocamerocertidae, which dominate the Middle Canadian, persist into the Upper, and become highly specialized, as shown by the siphuncle of *Proterocameroceras* itself. Even more bizarre specializations are found in *Meniscoceras*, the only known survivor of the Proterocameroceratidae in the Chazyan.

The Chazyan marks the appearance of a new stock, the Endoceratidae. This family contains longiconic shells, among which are to be found the largest of our straight cephalopods. They differ from the Proterocameroceratidae and agree with the Piloceratidae in possessing holochoanitic septal necks with the connecting rings within (Fig. 1D). This structural agreement suggests that perhaps the Endoceratidae may have descended from the Piloceratidae rather than from the Proterocameroceratidae which they resemble more superficially. Examination of the morphological facts with this possibility in mind yields some corroborative evidence. The true piloceroids are compressed. Although Endoceratidae are dominantly depressed in section in the adult, the early stages are dominantly, if not uniformly, compressed. Further, among the first of the true Endoceratidae are found those peculiar early stages which have long gone under the generic name *Nanno*. Schindewolf suggested that *Nanno* represented a retention of a preseptal phase, harkening back beyond the point in evolution at which the shell could even be classed as a cephalopod, close to the archetypical mollusc. Yet strangely enough nothing similar to *Nanno* appears in the earlier sediments. *Nanno* ranges from Chazyan to Richmond. The only earlier cephalopod which suggests it at all is the little known *Mysticoceras* of Canadian age. Certainly *Nanno* puts in too late an appearance to be interpreted according to Schindewolf's suggestion. Instead, its stratigraphic position suggests that it may represent the recapitulation of a *Piloceras* stage in the development of the Endoceratidae.

Among undisputed Ellesmeroceratidae no apical ends of the siphuncles are known. Enough specimens approach close to the apex to suggest that the siphuncle was small and marginal from its very beginning. *Pachendoceras*, as noted above, may be an ellesmeroceroid instead of an endoceroid. One specimen (Ulrich, Foerste, Miller and Unklesbay 1944, Pl. 61, Fig. 4), was interpreted as a specimen bearing an annulated endocone. This interpretation is based upon the fact that the apically protruding siphuncle bears annuli which are more widely spaced than are those indicated farther orad by the preserved camerae, or, for that matter, by the adoral part of the siphuncle which extends orad of the camerae. The interpretation of this specimen as an apical end rests upon (1) its small size in relation to other representatives of the species and (2) the fact that septation commonly varies in the early stages of primitive endoceroids, and the difference in spacing of the septa does therefore, not necessarily indicate the conclusion drawn from this specimen by its describers.

In the Proterocameroceratidae a very similar apical end of a siphuncle was described by the writer (Flower, 1941) as "*Cameroceras*" *annuliferum* (Fig. 3D). The nature of the siphuncle wall proclaims this form a member of the Proterocameroceratidae. Subsequently collected material from the type locality indicates that the species is rather generalized in form, but is close to some of the more generalized species which have been assigned to *Cyptendoceras*. Further, a similar small siphuncle has been found in the early stages of an unquestionable *Cyptendoceras* from the Fort Ann region. Both specimens show a siphuncle which contracts slowly toward its tip, and in both there is the faintest suggestion of a very tiny apical bulbous inflation. These facts are significant to the present discussion mainly in indicating that in the Lower and Middle Canadian Ellesmeroceratidae and Proterocameroceratidae there is no indication of a siphuncle which expands rapidly and may even occupy the entire diameter of the apical part of the shell.

Apices of siphuncles are well known in the Piloceratidae, but are invariably free from the phragmocone. Here both the phargmocone and the siphuncle expand

very rapidly. Although the camerate region of the shell is very tiny in the apical region, the evidence suggests that in all three of the genera the phragmocone extends very close to the apex, if not completely to it. (Fig. 3A.)

The next stage in development is marked by a tendency for the adoral part of the siphuncle to become slender. Sometimes the siphuncle assumes a more slender form gradually, but in a few species the transition is abrupt. Further, in these same species there is only poor and inconclusive evidence of septation on the outside of the siphuncle; such faint annuli as exist may be septa; on the other hand similar markings would be expected as relics of septa in shells in which the siphuncle has expanded so as to crowd out the camerae completely. Although such a conclusion is somewhat venturesome, I have indicated it in my interpretation of

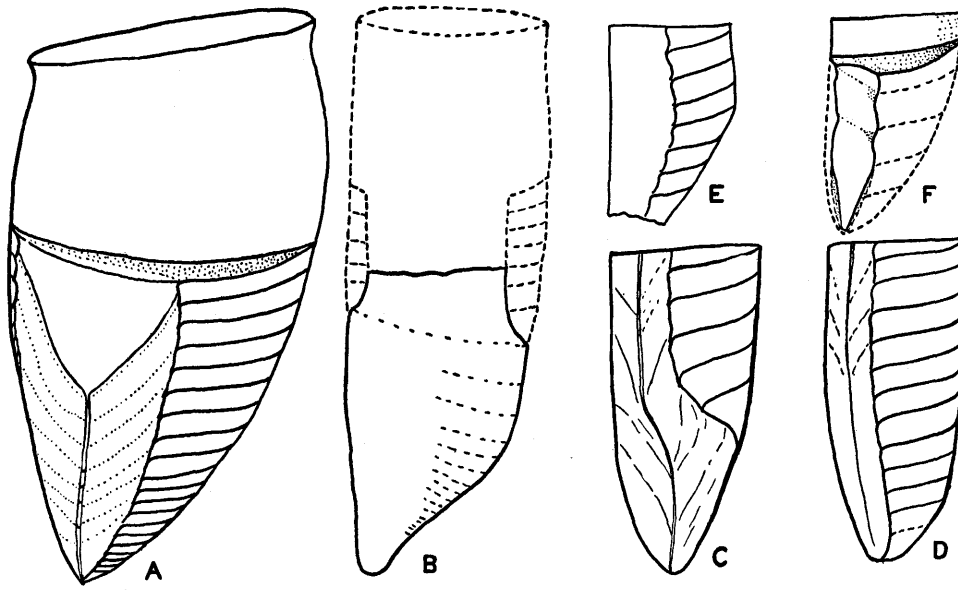

FIG. 3. Apical condition of siphuncles in endoceroids. A. *Cassinoceras*, with entire phragmocone expanding rapidly, but marked acceleration in expansion of siphuncle beyond that of the conch. B. *Allopiloceras*, based upon the specimen of *A. sevierense* showing the most marked adoral contraction of the siphuncle. Phragmocone and living chamber reconstructed. C. Vertical section through *Nanno*, based upon *N. noveboracum* Ruedemann. D. Apex of *Cyptendoceras annuliferum* (Flower). E. *Suecoceras*. F. Apex of *Endoceras*, based upon specimens currently assigned to *Cameroceras trentonense*. Shell restored over apex.

Allopiloceras (Fig. 3B), based upon a specimen of *A. sevierense* (Ulrich, Foerste and Miller, 1943, Pl. 3, Fig. 4), and have ventured to reconstruct a hypothetical phragmocone and living chamber for this species.

If such an apex is reduced in size, and the slender siphuncle indicated in this *Allopiloceras* is continued through a series of camerae in a slender phragmocone, a condition is developed which is essentially that of *Nanno noveboracum* Ruedemann (1906) of the Chazyan limestone (Fig. 3C). On this basis it is possible to explain *Nanno* as a recapitulation of a *Piloceras* stage, and the Piloceratidae-Endoceratidae sequence as a palingenetic one. *Nanno* persists into the Richmond, where a number of fine siphuncles, soon to be described, have been found. Some of these are startingly similar in proportions to those siphuncles which Holm (1896,) figured for *Nanno belemnitiforme* of the *Orthoceras* limestone of Sweden.

Continuation of the tachygenetic sequence would explain *Suecoceras* (Fig. 3E), as a slight reduction of the *Nanno* phase; the apex of the siphuncle is still swollen

and then contracted into a slender tube, but septation reaches the apex of the conch. Reduction of the swelling produces the apical ends which have been known as *Cameroceras* (Fig. 3F), and *Foerstella*. The genotype of *Foerstella* shows by the structure of the siphuncle wall that it is a true member of Endoceratidae. I have as yet had no material for sections of the type of *Cameroceras*, but there can be little doubt but that *Cameroceras trentonense* is nothing more than the apical stage of several species of *Endoceras* which occur as adult shells, though devoid of the apex, in the same beds. Among these forms is *Endoceras proteiforme*, the genotype.

Features of the endosiphuncle remain fairly uniform in the Endoceratidae, and differ from those of the Piloceratidae only in the simplification of the form of the endocones, which lack the wrinkling sometimes found in *Cassinoceras*. No important difference is to be found in the siphuncle walls between the two families. Yet the differences in shape are so great that the relationship was not previously suspected. However, it is now apparent that not only are there strong structural bonds uniting these two families, but that the slender endoceroids of the Canadian, which resemble the Endoceratidae superficially, differ from them widely in structure.

CONCLUSIONS

The morphological evidence yielded by thin sections of siphuncle walls shows that the holochoanitic type of structure is not dominant in a large group of cephalopods of which the endoceroids are a part, but instead is a specialization which is developed only in a small and highly specialized group of the Endoceratida, comprising the families Piloceratidae and Endoceratidae. The beginning of the stock is to be found in the oldest of our cephalopods, the ellesmeroceroids, which lack endocones, occasionally possess diaphraghms, but possess short septal necks supplemented by thick connecting rings. The Proterocameroceratidae, the first and simplest of the true endoceroids, differ from the ellesmeroceroids mainly in the addition of endocones to a shell which is otherwise essentially that of an ellesmeroceroid. Within the Proterocameroceratidae two trends are evident, first, the differentiation of parts of the connecting ring, producing either a zonal pattern or an eyelet. Happily connecting links are found showing that the two structural types are closely related. Second, in this family there is a tendency toward elongation of the septal necks. Necks long enough to be holochoanitic are found first in the Piloceratidae, accompanied by connecting rings, clearly a heritage from their ancestors of the Proterocameroceratidae. The rapid expansion of the piloceroid shell is necessarily coenogenetic. The Endoceratidae of the Ordovician are descended from the Piloceratidae with which they agree in the holochoanitic siphuncles retaining connecting rings. The rapid expansion of the siphuncle and the compressed condition of the piloceroid are recapitulated in the early stages of the Endoceratidae as shown by *Nanno*. Tachygenetic reduction of this stage produces more generalized early stages typified by *Cameroceras* and *Foerstella*. In gross features such apical ends resemble those of the Ellesmeroceratidae and Proterocameroceratidae, but differ from them in the holochoanitic septal necks.

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